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Macroinvertebrate Diversity and Rarity in Non-Glacial Alpine Streams

R Alther[1, 3], C Thompson[2], B Lods-Crozet[4] and CT Robinson[1]

1. Department of Aquatic Ecology, Eawag, Swiss Federal Institute of Aquatic Science and Technology, 8600 Dübendorf, Switzerland, and the Institute of Integrative Biology, ETH Zurich, Zurich, Switzerland.
2. Department of Environmental Sciences, Western Wyoming Community College, Rock Springs, Wyoming, USA.
3. Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, Switzerland.
4. Musée cantonal de Zoologie, Place de la Riponne 6, 1014 Lausanne, Switzerland.

Correspondence: robinson@eawag.ch

Running Head: Biodiversity in Alpine Streams

Abstract

Alpine landscapes are being transformed through the rapid recession of glaciers, resulting in the development of numerous non-glacial headwater streams inhabited by a diverse assemblage of macroinvertebrates. We examined spatial patterns in biodiversity and rarity of macroinvertebrates in 41 non-glacial streams from five glacierized catchments in the Swiss Alps undergoing rapid glacial recession over the last decades. Water physico-chemistry and food resources (periphyton, benthic organic matter) varied widely among streams within each catchment, while no significant differences occurred among catchments. Variability in community composition was similar among streams within each catchment but differed among catchments, reflecting differences in catchment-scale species pools due to biogeographical context and season. Overall, 101 taxa from ca 33,000 individuals collected were identified in the streams with 7 to 33 taxa found in individual streams. Some 64% of the taxa comprised less than 5% of the total abundances at the streams (rare in abundance) with 78% of the taxa being represented by less than 5% of the most common taxon (*Baetis* sp.), whereas 47% of the taxa were found in less than 10% of the streams (rare in distribution). No taxon was found at all sites (maximum presence at 85% of the sites), while 15% of the taxa were found at 50% of the sites or more. However, analyzing the rank-abundance distribution showed that rarity was less prevalent than previously shown in other ecosystems. The results indicated that community assembly of alpine headwater streams is a complex interaction between environmental properties (habitat filtering), habitat stability coupled with dispersal (source sink dynamics), and time since deglaciation (island biogeography). Integrating these processes is essential towards understanding ongoing colonization events in headwater streams of alpine catchments as glaciers continue to recede.

Key words: aquatic macroinvertebrates, dispersal, stream headwaters, species abundance distribution, community ecology, rarity

Introduction

Globally, alpine landscapes are undergoing major transformations in response to rapid glacial recession and altered precipitation patterns due to environmental change (IPCC 2014). Alpine catchments encompass a diversity of stream types, comprising strictly pro-glacial (kryal), groundwater-fed (krenal), and precipitation-fed (rhithral) streams (Milner and Petts 1994; Ward 1994), as well as streams with combinations of those water sources (Brown et al. 2009). In addition, streams differ in their water availability throughout the course of the year, including permanent streams but also intermittent/ephemeral streams (Robinson and Matthaei 2007; Brown et al. 2009; Robinson et al. 2015). Many alpine streams lengthen as glaciers retreat, glacial-fed streams in particular (Finn et al. 2010; Robinson et al. 2014), and new tributary streams and even proglacial lakes can develop (Milner et al. 2009).

Although a relatively recent research area (essentially beginning in the late 1990s), most stream research in alpine catchments has focused on glacial streams (see Milner et al. 2001; Jacobsen et al. 2012) with only a handful of studies examining other stream types (e.g., Fureder et al. 2001; Hieber et al. 2005; Cauvy-Fraunie 2014; Robinson et al. 2015). Stream intermittency can impose limitations on stream biodiversity (Datry et al. 2014), but permanent non-glacial (kreno-rhithral) streams likely enhance the overall biodiversity of alpine catchments by providing more optimal environmental conditions for aquatic insects than glacial and intermittent streams (Fureder et al. 2001; Hieber et al. 2005; Clitherow et al. 2013). Presently, there is major concern that changes in the eco-hydrology of glacial streams from climate change threaten the

65 biodiversity of alpine catchments via the loss of alpine specialists (Balint et al. 2011; Jacobsen et
66 al. 2012; Finn et al. 2013; Cauvy-Fraunie et al. 2016).

67 The dendritic structure of streams across landscapes often influences spatial biodiversity
68 patterns (Campbell Grant et al. 2007; Altermatt et al. 2013; Tonkin et al. 2018). This effect
69 should be pronounced in alpine catchments in which mainstem channels are typically glacial-fed
70 and therefore harsh environments due to unstable channels and cold temperatures (Fureder 1999;
71 Milner et al. 2001). These environmental factors constrain species distribution and abundance
72 (Clitherow et al. 2013; Cauvy-Fraunie 2014). In fact, species endemism is common in alpine
73 streams (Ward 1994; Robinson et al. 2010) and dispersal likely limited between stream types
74 (i.e., following source sink dynamics) (Finn et al. 2013; Cauvy-Fraunie et al. 2015). Further,
75 immigration is fed mostly from downstream sources, with species ranges moving upstream as
76 glaciers recede (Finn et al. 2010; Robinson et al. 2014). In this context, permanent tributaries
77 may act as stepping stones and continuous sources of immigrants for the colonization of other
78 non-glacial streams in alpine landscapes (Shama et al. 2011), and in particular streams emerging
79 during ongoing and rapid glacial recession. These newly colonized streams in turn may impose
80 strong environmental sorting mechanisms in the beginning that select for adapted specialist
81 species. This dynamic interplay has its roots in island biogeography theory (i.e., immigration and
82 extinction processes; MacArthur and Wilson 1967) placed within a habitat template framework
83 (sensu Southwood 1977, 1988).

84 Rarity is a common feature in the distribution and abundance of organisms in ecosystems
85 (Brown 1984; Gaston 1994; Brown et al. 1996; Magurran and Henderson 2003). Rabinowitz
86 (1981) described seven forms of rarity that are related to restricted geographic distribution,
87 narrow habitat distribution, and low local population abundance. Gaston and Fuller (2007) noted

88 that the presence of a few common species is a further type of rarity in community assembly, and
89 likely important in structuring biodiversity patterns among alpine streams (e.g., Clitherow et al.
90 2013). Indeed, rarity is often equated with the relationship between geographic range size and
91 dispersal (Lester et al. 2007). The high spatio-temporal heterogeneity in the habitat template of
92 alpine streams (e.g., Tockner et al. 1997) suggests that rarity may be an important component in
93 community assembly.

94 The contribution of rarity in the biodiversity of alpine streams has yet to be determined,
95 although food webs of glacial streams appear simple and dominated by a few common species
96 (Clitherow et al. 2013). Other studies have documented the presence of rare taxa in streams with
97 rarity ranging from ca. 37 to 75% of macroinvertebrate community composition (Resh et al.
98 2005; Arscott et al. 2006; Robinson et al. 2016). Further, how different stream types may interact
99 regionally in species distribution is still unclear. Rarity may act as a spatially shifting mosaic of
100 taxa presence in close vicinity to receding glaciers through a complex interplay of mass effects
101 and habitat filtering related to distance to the receding glacier (sensu Cottenie 2005). Newly
102 appearing streams next to the receding glacier may quickly be colonized by specialist species but
103 later harbor mostly generalist species since disturbance favors generalist species (Büchi and
104 Vuilleumier 2014). Work in arctic regions showed that less stable snowmelt-fed streams may
105 lose specialist species (Docherty et al. 2018) and extreme hydrological events and flow
106 variability impose strong effects on community assembly, favoring generalist species
107 (Sarremejane et al. 2018).

108 The primary objective of this study was to examine the biodiversity and rarity of
109 macroinvertebrates in tributary streams in alpine catchments undergoing rapid glacial recession.
110 Study streams lacked a glacial influence (i.e., kreno-rhithral) and had permanent flow, thus

providing more optimal environmental conditions for aquatic macroinvertebrates than so-called harsh pro-glacial and intermittent streams (Ward 1994). We hypothesized that (1) tributary streams show a large variation in environmental conditions with comparable variability within and between catchments, and house a diverse macroinvertebrate community, even though having low primary production and allochthonous inputs. (2) These environmental differences in physico-chemical variables and productivity will drive observed community differences. Unlike previous studies, we expected to find a deficiency of rare species in the study streams due to prevalent benign conditions (e.g., water temperature) in comparison to nearby glacial-fed streams and in combination with seasonal changes (Mykrä and Heino 2017). We further hypothesized that (3) the rank abundance distributions in these streams fit a log-normal distribution, with no excess of rare species. However, (4) the fraction of rare species was expected to be higher in younger streams closer to the retreating glacier due to the advantage of specialized species in colonizing these developing habitats, later to be replaced by generalist species (Sgarbi and Melo 2018).

Methods

Study sites

We selected five alpine catchments in Switzerland (Fig. 1) that contribute to three major drainage basins in Europe: Rhine River flowing to the North Sea, Rhone River flowing to the Mediterranean Sea, and the Inn/Danube River flowing to the Black Sea. The glaciers in each catchment have receded dramatically in the last decades; e.g., the Roseg glacier receded over 4 km from 1855 to 2011 and the Morteratsch glacier receded over 2.4 km from 1878 to 2011 (Burga 1999). In the last 50 years, Stein glacier receded 503 m, Lang glacier 572 m, Morteratsch 986 m, and Roseg receded 2663 m (data generated from Gletscherberichte 1881-2009). Glacial

134 recession has resulted in the emergence and lengthening of new stream channels and the
135 presence of pro-glacial lakes (Finn et al. 2010; Robinson et al. 2014).
136 Study streams in each catchment were first and second order headwater streams
137 situated between 1798 and 2494 m above sea level (a.s.l.) (Table 1) with permanent flow and
138 surrounded by sparse riparian vegetation and alpine pastures with small shrubs (mostly *Salix* and
139 *Alnus* spp.). The number of streams sampled in each catchment ranged from 5 (Morteratsch) to
140 8-10 (other catchments) (Fig. 1), totaling 41 tributaries. Sampling took place from mid-June to
141 early September 2012. The water source for each stream was groundwater and precipitation (rain
142 and snow-melt fed)(krenal/rhithral streams); and importantly, no stream was fed by glacial
143 meltwater (kryal streams) since there were no glaciers upstream potentially feeding into the
144 sampled streams (also see Fig. 1). All streams flowed into the main glacial-fed channel draining
145 each catchment and no stream was directly flow-connected to another study stream, meaning that
146 aquatic organisms dispersing between them must cross the main glacial-fed channel.
147 Representative 30-50 m reaches were sampled upstream of any physical influence of the
148 confluence with the glacial main channel; i.e., at least 100 m or more upstream of the confluence
149 depending on access to a stream. Each site location was recorded with a Garmin eTrex Vista
150 GPS device. Time since deglaciation was calculated with glacial recession data from the
151 Gletscherberichte (1881-2009). The time since deglaciation is a rough estimate since it is the
152 direct distance from the glacial snout compared to receding data and it assumes constant glacial
153 recession.
154
155 **Field and laboratory protocols**

156 At each site, we collected a 0.5 liter water sample for chemical analysis in the laboratory.
157 In the laboratory, water samples were analyzed for dissolved organic carbon (dorc), ortho-
158 phosphate (opho), dissolved phosphorus (dpho), total phosphorus (tpho), dissolved nitrogen
159 (dnit), nitrate (nitr), chloride (chlo), silicate (sili), sulfate (sulf), sodium (sodi), potassium (pota),
160 calcium (calc) and magnesium (magn) following methods detailed in Tockner et al. (1997). Most
161 values for dissolved nitrogen, nitrate, chloride, dissolved phosphorus, sodium, potassium,
162 calcium and magnesium were below detection limits of the analytical procedures and not
163 included in additional analyses. Spot recordings of temperature (temp), electrical conductivity
164 (cond) (WTW, Germany) and turbidity (turb) (Cosmos, Switzerland) were made with field
165 portable meters at each site. Discharge (disc) of each stream at the time of sampling was
166 estimated using width, depth and velocity (MiniAir 2, Schiltknecht AG, Gossau, Switzerland)
167 measures averaged across 20 transects (Allan and Castillo 2009).
168 Periphyton biomass as a measure of food resource availability was determined
169 quantitatively for each stream by collecting three randomly selected stones (b-axis: mean = 6.3
170 cm, SD = 1.4) and storing at -20°C for subsequent processing in the laboratory. Periphyton was
171 removed from the surface of each stone with a metal bristle brush and a 5-10 ml aliquot filtered
172 through a combusted GF/F Whatman™ filter. The filtered material was dried at 60°C, weighed,
173 ashed at 500°C for 4 hours, and reweighed for determination of ash-free dry mass (AFDM). Each
174 AFDM value was standardized to the surface of the corresponding stone ($a-axis \times b-axis \times$
175 $\pi/4$) (after Uehlinger 1991). Benthic organic matter (BOM), also as a measure of food resource
176 availability, was collected at three randomly selected locations in each stream. The collection
177 area (15x15 cm) was disturbed to a depth of 10 cm and the suspended material collected in a net
178 (mesh size = 250 µm) placed directly downstream. Samples were stored frozen (-20°C) and

179 analyzed later in the laboratory. After removing macroinvertebrates, the ash-free dry mass of
180 each sample was determined as for periphyton.
181 We used a circular kicknet (mesh size = 250 µm, diameter = 20 cm) for the qualitative
182 sampling of macroinvertebrates in each stream. Sampling was conducted for 5 minutes along the
183 study reach in each stream, sampling in a corresponding ratio of fast- to slow-flowing areas to
184 ensure coverage of the most common habitat types in each stream. The streambed was disturbed
185 manually, turning single stones and digging in the stream bottom to collect as many taxa as
186 possible inhabiting each stream. Macroinvertebrate samples were preserved with 70% ethanol for
187 later processing in the laboratory. In the laboratory, each sample was presorted, separating all
188 clearly visible individuals from the coarse organic matter such as leaf litter and branches.
189 Depending on the density of the most frequent taxon, a fraction of the sample was sorted using a
190 stereomicroscope. Individuals were handpicked from subsamples until a threshold of 50
191 individuals from the most frequent taxon was reached. All specimens were identified with a
192 Leica M205C or Olympus SZH-ILLB dissecting stereomicroscope and counted. For analysis,
193 individuals from the subsamples were up-scaled by the fraction and added to the total numbers.
194 Species keys used for identification were *Invertébrés d'eau douce* (Tachet et al. 2010),
195 *Ephemeroptera (Fauna Helvetica; 9)* (Studemann et al. 1992), *Die Steinfliegen der Schweiz*
196 *(Fauna Helvetica; 27)* (Lubini et al. 2012), *Atlas of Central European Trichoptera Larvae*
197 (Waringer and Graf 2011), and *Bestimmung wirbelloser Tiere* (Bährmann 2011). Chironomids
198 (larvae) were identified to species/genus and species groups (Wiederholm 1983, 1986; Serra-
199 Tosio 1989; Langton 1991; Schmid 1993; Saether 1995; Brooks et al. 2007; Lencioni et al. 2007;
200 Ilyashuk et al. 2010). A large majority of the chironomid material was mounted (microscopic
201 slides) in Euparal and all the collection material (slides and alcohol samples) deposited in the

Museum of Zoology in Lausanne (Switzerland) for archiving. Simuliidae were classified as either *Simulium* or *Prosimulium* spp. based on the coloration of antenna and the form of the frontoclypeus (Tachet et al. 2010). We identified the Plecoptera and Ephemeroptera to genus and Trichoptera to species, thereby allowing a tentative comparison with the official Swiss biodiversity monitoring data (IBCH method; Stucki 2010). All identified individuals, except chironomids, were stored in 70% ethanol as a reference collection at Eawag, Duebendorf, Switzerland.

Data analysis

All raw data are available in the Supplement Data S1. The environmental variables were tested for a normal distribution using a Shapiro-Wilk test. Except for temperature and silicate that met normality assumptions, variables were ln(x) or ln(x+1) transformed (Zar 1984). Following transformation, all variables meeting the assumptions of a normal distribution (temperature, silicate, elevation, conductivity, discharge, AFDM, BOM) were tested for significant differences among catchments using ANOVA and MANOVA using the Pillai–Bartlett statistic. Those variables not meeting a normal distribution (DOM, sulfate, ortho-phosphorus, total phosphorus) were excluded from further analysis. Environmental data also were analyzed using principal components analysis (PCA) to illustrate any basin or stream differences (Legendre and Legendre, 2012) using the function *princomp* in R.

Macroinvertebrate diversity was assessed using abundance data (individuals per 5-min kick sample) and taxon richness (as morphospecies). We calculated Simpson's Index (1-D) as $D = \sum \frac{n_i(n_i-1)}{N(N-1)}$, where n_i is the number of individuals of the i^{th} taxon and N the total number of individuals within the sample, and the Shannon-Weaver Index (H') as $H' = -\sum p_i * \ln p_i$, where

225 $p_i = n_i / N$ (Jost 2007) using the function *diversity* from package vegan (Oksanen et al. 2018).
226 These indices were calculated for each site and represent the classical α-diversity (after
227 Whittaker 1956). Taxa turnover between sites and catchments was assessed using βw-diversity
228 calculated as $\beta_W = \frac{\gamma - \alpha}{\alpha} = \frac{\gamma}{\alpha} - 1$ and is analogous to δ-diversity, where $\gamma - \alpha = \beta_A$ or the
229 absolute taxa turnover (Whittaker 1972; Koleff et al. 2003). Taxon accumulation curves were
230 generated using the function *specaccum* from package vegan, adding sites randomly and doing
231 100 permutations. Rank-abundance distributions were directly accessible from ordered raw
232 abundance data (after Kendall 1938). Rarity was calculated using a threshold value of 5% for
233 abundance rarity, defining species as being rare if represented by less than 5% of the total
234 number of sampled individuals or if represented by less than 5% of the individuals of the most
235 common taxon. Additionally, we defined taxa as being rare at sites if they were found in less
236 than 10% of the sampled sites (4 sites or less).
237 Distance matrices for the community data were calculated from absolute numbers using
238 the Bray-Curtis index (Bray and Curtis 1957) using the function *vegdist* from package vegan. We
239 performed a nonmetric dimensional scaling analysis (NMDS) to examine for community
240 differences among catchments. The number of dimensions was chosen such that the stress values
241 were below 0.05. To statistically check for differences between communities present among
242 catchments, we used an analysis of similarity (ANOSIM) (Anderson 2001) using the function
243 *adonis* from package vegan. To assess the potential influence of environmental variables on
244 community composition, we performed a distance-based redundancy analysis (dbRDA;
245 Legendre and Anderson 1999) using the function *dbrda* from package vegan. Since two
246 measures were missing, we only considered 39 sites and temperature, silicate, elevation,
247 conductivity, discharge, AFDM, and BOM as explanatory environmental variables.

To assess differences in β-diversity, we performed a multivariate test of homogeneity of dispersions (PERMDISP; Anderson 2006) using the function *betadisper* from package vegan. We assessed statistical significance of the result using a permutation test with 999 runs. To compare the observed rank-abundance distribution to theoretical log-normal and log-series distributions, we generated the expected distributions using 999 simulated draws from these distributions either providing the observed mean and standard deviation (for log-normal, *rlnorm*) or Fisher's alpha (Fisher et al. 1943), derived with the function *fisherfit* from package vegan (for log-series *rls* from package sads). To statistically assess, if our abundance data fit a log-normal distribution we performed a Shapiro-Wilk test of the log-transformed data.

To test if distance to the glacier had an influence on the fraction of rare species at single sites, we ran a generalized linear model with log-transformed distance to glacier snout assuming a quasi-binomial response. Since assuming a quasi-binomial response is only an approximation, we ran a Beta regression assuming a beta-distributed response with the function *betareg* from package betareg (Cribari-Neto and Zeileis 2010). Package versions were ver 2.4-6 for vegan (Oksanen et al. 2018) and ver 3.1-0 for betareg (Cribari-Neto and Zeileis 2010). All statistical analyses were performed using R 3.4.4 (R Core Team, 2018) and R Studio ver. 1.1.442 (© 2009-2018, R Studio, Inc.). The whole R script used for analysis is available in the Supplement Data S2.

Results

Environmental characteristics of streams

All streams had clear water at the time of sampling with turbidity <10 NTU (Table 1). Mean site elevation was 2080 m a.s.l. (SD 154 m a.s.l.) with the lowest stream at 1798 m a.s.l. (Lang) and the highest (2495 m a.s.l.) at Jöri (Table 1). The mean discharge of streams was

271 generally low, ranging from 0.08 (Stein) to 0.33 (Morteratsch) $m^3 s^{-1}$, although varying
272 considerably among streams (CV = 166%). Mean conductivity was low at 45.5 µS cm^{-1} (SD 24.7
273 µS cm^{-1}), ranging from 21.1 (Morteratsch) to 63.4 (Lang) µS cm^{-1}. Mean stream temperature was
274 8.2°C (SD 3.5°C) and mean silicate concentration was 4.94 mg L^{-1} (SD 1.85 mg L^{-1}). Mean
275 BOM was 0.42 g AFDM (SD 0.41 g) among catchments. Mean periphyton biomass (AFDM)
276 was 34.3 g m^{-2} (SD 24.5 g m^{-2}). All values are summarized in Table 1.
277 Significant differences were found among catchments for temperature, silicate, and
278 elevation (ANOVA, $F_{4,36}$ = 4.18; 4.07; 5.45, all $p < 0.01$). The other variables (conductivity,
279 discharge, AFDM, BOM) were not significantly different among catchments (ANOVA, $p >$
280 0.05). MANOVA confirmed the overall environmental differentiation among catchments
281 (approx. $F_{4,34} = 3.11$, $p < 0.001$). A PCA-ordination containing all environmental variables
282 showed these subtle differences of stream environmental properties among the different
283 catchments (Supp. Fig. S1).
284
285 **Biodiversity patterns**
286 Overall, 101 aquatic taxa representing 12 taxonomic orders were identified from the
287 33,150 collected individuals from the 41 streams. Average taxa richness per site was 21.8 (SD
288 7.1), with a minimum of 7 taxa (Lang) and maximum of 33 taxa (Lang). The number of sites
289 occupied per taxon ranged from 1 (*Amphinemura* sp.) to 35 (*Baetis* sp.) (mean 8.9, SD 8.9).
290 Abundance within streams ranged from 18 to 2539 (both in Lang) individuals per kick sample
291 (mean 808.5, SD 667.2) (Table 2).The mean number of individuals per species was 328.2 (SD
292 764.9), and ranged from 1 (e.g. Hydrophilidae) to 5643 (*Baetis* sp.). The taxon accumulation

293 curve showed that there were a few more species to be expected if our sampling was continued
294 (Supp. Fig. S2).
295 The number of taxa and abundance of individuals did not differ significantly between
296 catchments (ANOVA, $F_{4,36}$ = 1.66 and 0.051, p = 0.18 and 0.99, respectively). Mean catchment
297 values for Shannon's H' ranged from 1.88 (Roseg) to 2.35 (Jöri), and for the Simpson's index
298 from 0.72 (Roseg) to 0.85 (Jöri). Mean catchment $ß_w$-diversity (beta diversity) ranged from 0.43
299 (Jöri) to 0.60 (Lang) and ranged from 0.22 to 0.88 among streams within a catchment. Mean
300 catchment $ß_a$ (absolute taxa turnover) ranged from 10.4 (Morteratsch) to 12.6 (Jöri) (Table 2).
301 Shannon's H' and Simpson's index (1-D) were not significantly different among catchments
302 (ANOVA, $F_{4,36}$ = 1.22 and 0.73, p = 0.32 and 0.58, respectively).
303 Most individuals were Diptera and EPT taxa (Ephemeroptera/Plecoptera/Trichoptera).
304 Around 95% of the identified individuals were represented by the 36 most abundant taxa,
305 indicating that the other 65 taxa (64%) were rare in abundance. Some 47 taxa (47%) would be
306 considered rare when defining rarity as those taxa occurring only at a few sites (present at <10%
307 of the sites; i.e., present at 4 sites or fewer). Twenty taxa occurred only at one site, whereas a
308 different set of 15 taxa were found at 50% of the sites or more. No taxon was found at all sites
309 (maximum number sites for presence was 35 (85%) for *Baetis alpinus* (Ephemeroptera) and
310 *Pediciini* (Diptera).
311 A nonmetric multidimensional scaling (NMDS) with 8 dimensions and Hellinger
312 transformed community data separately grouped streams among catchments (Fig. 2). The
313 catchments of Morteratsch, Roseg and Lang overlapped along axis 1 and 2. These results were
314 confirmed by the analysis of similarity (ANOSIM), showing subtle but significant differences

among catchments based on Bray-Curtis community dissimilarity (R = 0.33, $p < 0.001$; Supp. Fig. S3).

The distance-based redundancy analysis using Hellinger-transformed community data and the environmental data showed that there was a significant effect of environmental variables on community dissimilarity (permutation test, $F_{7,31} = 1.52$, $p = 0.003$; Fig. 3). A permutation test adding terms sequentially showed that these differences were explained mostly by differences in temperature and elevation.

The PERMDISP analysis (Supp. Fig. 4) to assess community divergence showed that there was no significant difference in β-diversity between catchments (permutation test, $F_{4,34} = 1.38$, $p = 0.26$). This result suggests that community variance (β-diversity) within catchments is comparable to between catchment variance. Only the comparison between Jöri and Lang revealed a significant community divergence (permutation test, $F_{4,34} = 1.38$, observed $p = 0.046$).

The comparison of observed rank-abundance distribution to the theoretically expected log-normal or log-series distributions showed that our community data were log-normal distributed (Fig. 4). This result indicates that there were less rare species than previously shown in many ecosystems (Magurran and Henderson 2003). However, the Shapiro-Wilk test on the log-scale showed that the abundance data did not exactly fulfill the assumptions of log-normal (W = 0.969, $p = 0.019$). Checking the histogram of log-transformed abundance data (Supp. Fig. S5) showed that there was an excess of single findings and a slight excess of very common species, which also is visible in the log-normal QQ-plot (Supp. Fig. S6).

The time (in years) since study streams emerged from beneath retreating glaciers was highly correlated with the actual spatial distance to the glacial snout (Spearman's rho = 0.92; $p < 0.0001$) and so distance can be used as a surrogate for stream age. A quasi-binomial GLM

confirmed our assumption that the fraction of rare species decreased with increasing distance of the sampling site from the glacier ($p < 0.001$; Fig. 6). Beta regression supported this result, showing a highly significant response ($z = 4.18$, $p < 0.001$), even though the Pseudo R^2 was only 0.374 (Fig. 5).

Discussion

Globally, alpine landscapes are being transformed at unprecedented rates concomitantly with rapid glacial recession. How this rapid environmental transformation influences the distribution and abundance of aquatic macroinvertebrates is a key question regarding future trajectories in biodiversity within these landscapes (e.g., Leys et al. 2016). Current thinking infers a biodiversity crisis with major reductions in beta diversity (Jacobsen et al. 2012; Finn et al. 2013), reflecting losses in cryptic species and genetic diversity of macroinvertebrates in general (Balint et al. 2011; but see Isaak et al. 2016). The dendritic nature of stream networks strongly affects the dispersal of aquatic organisms across the landscape (Altermatt et al. 2013; Wilson and McTammany 2016), especially in alpine landscapes in which the harshness of glacial mainstem channels limits dispersal of truly aquatic species among tributary streams (see Cauvy-Fraunie et al. 2015). This critical constraint on macroinvertebrate dispersal in glacierized catchments infers the important role of rarity in biodiversity patterns within and among non-glacial tributary streams (sensu Kunin and Gaston 1993). Our results document that rarity is less prevalent than in other ecosystems and hence generalist species likely play an important role in the ecology of non-glacial alpine streams and in the overall biodiversity of glaciated alpine catchments.

As expected, rarity contributed to the α-diversity within the sampled streams, contributing upwards of 90% to the overall biodiversity within individual streams. In terms of

abundance, 65 of 101 identified taxa represented < 5% of the total abundance when all streams were considered. Indeed, no taxon was found at all sites (maximum presence was 35 of 41 sites), whereas 47 taxa were found at <10% of the sites. This pattern of diversity fits general theory in which a strong correlation exists between abundance and occupancy (after Gaston et al. 2000) and also fits abundance patterns of diatoms (Robinson et al. 2010) and bacteria (Besemer et al. 2013) in alpine headwaters. Chironomidae dominated most stream assemblages in terms of abundance (see Robinson et al. 2010; Robinson et al. 2016), and are usually the first to colonize newly developed proglacial streams (Finn et al. 2010; Robinson et al. 2014). Lencioni et al. (2011) found 67% of the chironomids identified in their study were rare, thus showing a similar pattern as this study in terms of overall rarity. Typically, a few common species (i.e., rarity in commonness) maintain ecosystem function (Smith and Knapp 2003; but see Leitao et al. 2016 for an alternate view), whereas the commonness of rare species (in terms of abundance) increases the invasibility of ecosystems (Lyons and Schwartz 2001). In this respect, the expected threat to biodiversity through the loss of rare species, and endemic specialists in particular, may enhance invasion of these systems by other species (e.g., those expanding their upstream distribution with glacial recession, see Finn et al. 2010). How these new species influence future trends in ecosystem function, e.g. functional diversity or redundancy (see Leitao et al. 2016; Logares et al. 2016), has yet to be determined.

Many of the taxa involved were aquatic insects and had a flying adult stage in the life cycle, thus allowing overland dispersal between streams. Cauvy-Fraunie et al. (2015) found that dispersal in glaciated catchments was restricted by the harsh environmental conditions of glacial mainstem channels into which non-glacial streams flow, thus restricting active dispersal among alpine streams to primarily aquatic insects with a flying adult stage (also see Thompson and

384 Townsend 2006 for similar ideas regarding species traits and dispersal limitations). This
385 dispersal pattern follows that described by stepping stone models and source sink dynamics
386 (Finn et al. 2014; Finn et al. 2016). Non-glacial streams likely are colonized first by migrants
387 from adjacent or nearby non-glacial streams as stepping stones (Shama et al. 2011). Likewise,
388 immigrants attempting to colonize the environmentally harsh glacial mainstem or nearby
389 temporary alpine streams probably fail to maintain adequate populations and the channel/streams
390 can thus act as a sink for these organisms (e.g. Tonkin et al. 2016a,b). For instance, Shama et al.
391 (2011) documented strong bottleneck effects in the spatial genetic structure of a caddisfly
392 between permanent and temporary alpine streams. Leys et al. (2016) also showed distribution
393 differences between cryptic species of the alpine mayfly *Baetis alpinus*, the most common taxon
394 (abundance and distribution) in the current study.
395 Despite subtle differences in stream environmental conditions that reflected regional
396 differences in geology, e.g. between Stein catchment and the other catchments, this was not
397 reflected directly in community composition. Consequently, the mean beta ($ß_w$) diversity was
398 similar among catchments, although varying substantially among streams within a catchment,
399 suggesting similar community assembly processes were operating within the different
400 catchments (see Tonkin et al. 2016b regarding mass effects vs. species sorting processes in river
401 networks). Due to the sampling campaign being conducted in a single season, temporal variation
402 could not be studied and future studies are needed to understand this aspect, potentially being
403 pronounced in non-glacial tributaries.
404 Future environmental trajectories predict the continuing loss of glaciers in many alpine
405 catchments worldwide (IPCC 2014) with a concomitant reduction in glacial influence on the
406 ecohydrology of river networks (Huss et al. 2008; Sorg et al. 2012). Furthermore, the projected

407 degree of climate change is expected to be greater at higher altitudes due in part to a
408 proportionately larger decrease in snow cover (IPCC 2014). A recent global study by Ohmura
409 (2012) based on observations from the last 50 to 125 years found enhanced warming with
410 elevation in about two-thirds of the mountain regions examined. Additionally, various studies
411 have documented a high degree of stream intermittency due to seasonal expansion and
412 contraction cycles in the hydrology of alpine landscapes (Malard et al. 2006; Robinson and
413 Matthaei 2007; Robinson et al. 2015) with the degree of intermittency likely to increase in the
414 future (Robinson et al. 2003; Datry et al. 2014). The reduction in glacial influence will likely
415 enhance the dispersal potential of macroinvertebrates among alpine streams by allowing more
416 species to disperse via mainstem channels (sensu Cauvy-Fraunie et al. 2015) but also provide
417 more optimal environmental conditions for immigrants from downstream to colonize permanent
418 alpine streams (Finn et al. 2010; Cauvy-Fraunie et al. 2016). The more favourable and connected
419 tributary habitats may even enhance biological invasion by non-native species.
420 The observed pattern of abundance seems to imply that there is a surplus of generalist
421 species, with less rare species than would be expected in comparison to other ecosystems. The
422 effects of this interplay (habitat homogenization and intermittency versus dispersal and
423 colonization) on alpine stream biodiversity is unknown but suggests that both generalist and
424 specialist species will still be important as some species are lost while others redistribute through
425 dispersal and immigration (sensu MacArthur and Wilson 1967). Species presence and absence
426 among streams will be a function of local habitat conditions (sensu Southwood 1977, 1988) with
427 a few common taxa (some rare taxa as well becoming common) dominating community
428 assemblages and ecosystem functioning (after Gaston and Fuller 2007). Lastly, only a small
429 fraction of rare species will potentially change their status at a given site over time (Magurran

and Henderson 2003; Sgarbi and Melo 2018). Regardless, regional species pools will likely decrease with loss of endemic, alpine and glacier stream specialists (Jacobsen et al. 2012) along with the loss in cryptic species and overall genetic diversity (Balint et al. 2011; Pauls et al. 2013; Finn et al. 2014). As suggested by Lennon et al. (2004) for birds, patterns of richness may be explained better through the spatial distribution of the few common species in the ecosystem and their response to environmental change on stream structure and function.

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Literature Cited

Allan JD, Castillo MM (2009) Stream Ecology: Structure and Function of Running Waters. Springer, Dordrecht, The Netherlands

Altermatt F, Seymour M, Martinez N (2013) River network properties shape alpha-diversity and community similarity patterns of aquatic insect communities across major drainage basins. Journal of Biogeography 92: 859–870

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecology 26: 32–46

Anderson MJ (2006) Distance-based tests for homogeneity of multivariate dispersions. Biometrics 62: 245–253

454 Arscott DB, Jackson JK, Kratzer EB (2006) Role of rarity and taxonomic resolution in a regional
455 and spatial analysis of stream macroinvertebrates. Journal of the North American
456 Benthological Society 25: 977–997
457 Bährmann R (2011) Bestimmung wirbelloser Tiere. (R. Bährmann, Ed.) (6. Edition). Heidelberg:
458 Spektrum Akademischer Verlag
459 Balint M, Domisch S, Engelhardt CHM, Haase P, Lehrian S, Sauer J, Theissinger K, Pauls SU,
460 Nowak C (2011) Cryptic biodiversity loss linked to global climate change. Nature
461 Climate Change 1: 313–318
462 Besemer K, Singer G, Quince C, Bertuzzo E, Sloan W, Battin TJ (2013) Headwaters are critical
463 reservoirs of microbial diversity for fluvial networks. Proceedings of the Royal Society B
464 280: 20131760
465 Bray JR, Curtis JT (1957) An ordination of the upland forest communities of southern
466 Wisconson. Ecological Monographs 27: 325–349
467 Brooks SJ, Langdon PG, Heiri O (2007) The identification and use of Palaearctic Chironomidae
468 larvae in palaeoecology. QRA Technical Guide n°10. Quaternary Research Association.
469 London.
470 Brown JH (1984) On the relationship between abundance and distribution of species. The
471 American Naturalist 124: 255–279
472 Brown JH, Stevens GC, Kaufman DM (1996) The geographic range: size, shape, boundaries, and
473 internal structure. Annual Review Ecology and Systematics 27: 597–623
474 Brown LE, Hannah DM, Milner AM (2009) ARISE: a classification tool for Alpine River and
475 Stream Ecosystems. Freshwater Biology 54: 1357–1369
476 Büchi L, Vuilleumier S (2014) Coexistence of specialist and generalist species is shaped by
477 dispersal and environmental factors. The American Naturalist 183: 612–624
478 Burga CA (1999) Vegetation development on the glacier forefield Morteratsch (Switzerland).
479 Applied Vegetation Science 2: 17–24
480 Campbell Grant EH, Lowe WH, Fagan WF (2007) Living in the branches: population dynamics
481 and ecological processes in dendritic networks. Ecology Letters 10: 165–175
482 Cauvy-Fraunié S (2014) Hydroecology of invertebrate communities in equatorial glacier-fed
483 streams. PhD thesis, Pierre Marie Curie University (Paris 6), France

484 Cauvy-Fraunié S, Andino P, Espinosa R, Calvez R, Jacobsen D, Dangles O (2016) Ecological
485 responses to experimental glacier-runoff reduction in alpine rivers. Nature
486 Communications 7: 12025
487 Cauvy-Fraunié S, Espinosa R, Andino P, Jacobsen D, Dangles O (2015) Invertebrate
488 metacommunity structure and dynamics in an Andean glacial stream network facing
489 climate change Plos one 10, e0136793
490 Clitherow LR, Carrivick JL, Brown LE (2013) Food web structure in a harsh glacier-fed river.
491 Plos one 8: 1–11
492 Cottenie K (2005) Integrating environmental and spatial processes in ecological community
493 dynamics. Ecology Letters 8: 1175–1182
494 Cribari-Neto F, Zeileis A (2010) Beta Regression in R. Journal of Statistical Software 34: 1–24
495 Datry T, Larned ST, Tockner K (2014) Intermittent rivers: a challenge for freshwater ecology.
496 BioScience 64: 229–235
497 Docherty CL, Hannah DM, Riis T, Lund M, Abermann J, Milner AM (2018) Spatio-temporal
498 dynamics of macroinvertebrate communities in northeast Greenlandic snowmelt streams.
499 Ecohydrology 11: 1–13
500 Finn DS, Encalada AC, Hampel H (2016) Genetic isolation among mountains but not between
501 stream types in a tropical high-altitude mayfly. Freshwater Biology 61: 702–714
502 Finn DS, Khamis K, Milner AM (2013) Loss of small glaciers will diminish beta diversity in
503 Pyrenean streams at two levels of biological organization. Global Ecology and
504 Biogeography 22: 40–51
505 Finn DS, Räsänen K, Robinson CT (2010) Physical and biological changes to a lengthening
506 stream gradient following a decade of rapid glacial recession. Global Change Biology 16:
507 3314–3326
508 Finn DS, Zamora-Munoz C, Murria C, Sainz-Bariaiin M, Alba-Tercedor J (2014) Evidence from
509 recently deglaciated mountain ranges that Baetis alpinus (Ephemeroptera) could lose
510 siginfiant genetic diversity as alpine glaciers dissappear. Freshwater Science 33: 207–216
511 Fisher RA, Corbet AS, Williams CB (1943) The relation between the number of species and the
512 number of individuals in a random sample of an animal population. The Journal of
513 Animal Ecology 12: 42–58

514 Fureder L (1999) High alpine streams: cold habitats for insect larvae. In: R. Margesin & F.
515 Schinner, eds. Cold Adapted Organisms. Ecology, Physiology, Enzymology and
516 Molecular Biology. Berlin: Springer-Verlag, pp. 181–196
517 Füreder L, Schutz C, Wallinger M, Burger R (2001) Physico-chemistry and aquatic insects of a
518 glacier-fed and spring-fed alpine stream. Freshwater Biology 46: 1673–1690
519 Gaston KJ (1994) Rarity. Chapman and Hall, London
520 Gaston KJ, Blackburn TM, Greenwood JD, Gregory RD, Quinn RM, Lawton JH (2000)
521 Abundance-occupancy relationships. Journal of Applied Ecology 37: 39–59
522 Gaston KJ, Fuller RA (2007) Commonness, population depletion and conservation biology.
523 Trends in Ecology and Evolution 23: 14–19
524 Gletscherberichte (1881-2009) "Die Gletscher der Schweizer Alpen", Jahrbücher der
525 Expertenkommission für Kryosphärenmessnetze der Akademie der Naturwissenschaften
526 Schweiz (SCNAT) herausgegegeben seit 1964 durch die Versuchsanstalt für Wasserbau,
527 Hydrologie und Glaziologie (VAW) der ETH Zürich. No. 1–126,
528 (http://glaciology.ethz.ch/swiss-glaciers/)
529 Hieber M, Robinson CT, Uehlinger U, Ward JV (2005) A comparison of benthic
530 macroinvertebrate assemblages among different types of alpine streams. Freshwater
531 Biology 50: 2087–2100
532 Huss M, Farinotti D, Bauder A, Funk M (2008) Modeling runoff from highly glaciaeriezed
533 alpine drainage basins in a changing climate. Hydrological Processes 22: 3888–3902
534 Ilyashuk B, Ilyashuk E, Makarchenko EA, Heiri O (2010) Midges of the genus *Pseudodiamesa*
535 Goetghebuer (Diptera, Chironomidae): current knowledge and palaeoecological
536 perspective. Journal of Paleolimnology 44: 667–676
537 IPCC (2014) Climate change 2014: Synthesis report. Cambridge University Press, Cambridge,
538 UK
539 Isaak DJ, Young MK, Luce CH, Hostetler SW, Wenger SJ, Peterson EE, Ver Hoef JM, Groce
540 MC, Horan DL, Nagel DE (2016) Slow climate velocities of mountain streams portend
541 their role as refugia for cold-water biodiversity. PNAS 113: 4374–4379
542 Jacobsen D, Milner AM, Brown LE, Dangles O (2012) Biodiversity under threat in glacier-fed
543 river systems. Nature Climate Change 2: 361-364

544 Jost L (2007) Partitioning diversity into independent alpha and beta components. Ecology 88:
545 2427–2439
546 Kendall MG (1938) A new measure of rank correlation. Biometrika 30: 81–93
547 Koleff P, Gaston K, Lennon JJ (2003) Measuring beta diversity for presence-absence data.
548 Journal of Animal Ecology 72: 367–382
549 Kunin WE, Gaston KJ (1993) The biology of rarity: patterns, causes and consequences. TREE 8:
550 298-301
551 Langton PH (1991) A key to pupal exuviae of West Palaearctic Chironomidae. Privately
552 published by P.H. Langton, 5 Kylebeg Av., Mountsandel, Cleraine, Co. Londonderry,
553 Northern Ireland
554 Legendre P, Anderson MJ (1999) Distance-based redundancy analysis: testing multispecies
555 responses in multifactorial ecological experiments. Ecological Monographs 69: 1–24
556 Legendre P, Legendre L (2012) Numerical Ecology, 3rd edition. Elsevier Publishing,
557 Amsterdam
558 Leitao RP, Zuanon J, Villeger S, Williams SE, Baraloto C, Fortunel C, Mendonca FP, Mouillot
559 D (2016) Rare species contribute disproportionately to the functional structure of species
560 assemblages. Proceedings of the Royal Society B 283: 20160084
561 Lencioni V, Marziali L, Rossaro B (2007) I Ditteri Chironomidi: morfologia, tassonomia,
562 ecologia, fisiologia e zoogeografia. Quaderni del Museo Tridentino di Scienze Naturali 1
563 Lencioni V, Marziali L, Rossaro B (2011) Diversity and distribution of chironomids (Diptera,
564 Chironomidae) in pristine Alpine and pre-Alpine springs. Journal of Limnology 70: 106–
565 121
566 Lennon JJ, Koleff P, Greenwood JJD, Gaston KJ (2004) Contribution of rarity and commonness
567 to patterns of species richness. Ecology Letters 7: 81–87
568 Lester SE, Ruttenberg BI, Gaines SD, Kinlan BP (2007) The relationship between dispersal
569 ability and geographic range size. Ecology Letters 10: 745–758
570 Leys M, Keller I, Räsänen K, Gattolliat JL, Robinson CT (2016) Distribution and population
571 genetic variation of cryptic species of the Alpine mayfly *Baetis alpinus* (Ephemeroptera:
572 Baetidae) in the Central Alps. BMC Evolutionary Biology 16:77
573 Logares R, Mangot J-F, Massana R (2016) Rarity in aquatic microbes: placing protists on the
574 map. Research in Microbiology 166: 831–841

Lubini V, Knispel S, Vinçon G (2012) Fauna Helvetica 27: Die Steinfliegen der Schweiz.

Lyons KG, Schwartz MW (2001) Rare species loss alters ecosystem functon – invasion resistance. Ecology Letters 4: 358-365

MacArthur RH, Wilson EO (1967) The Theory of Island Biogeography. Princeton University Press, Princeton, New Jersey

Magurran AE, Henderson PA (2003) Explaining the excess of rare species in natural species abundance distributions. Nature 422: 714–716.

Malard F, Uehlinger U, Zah R, Tockner K (2006) Floodpulse and riverscape dynamics in a braided glacial river. Ecology 87: 704–716

Milner AM, Petts GE (1994) Glacial rivers: physical habitat and ecology. Freshwater Biology 32: 295–307

Milner AM, Brittain JE, Castella E, Petts GE (2001) Trends of macroinvertebrate community strcuture in glacial-fed rivers in relation to environmental conditions: a synthesis. Freshwater Biology 46: 1833–1847

Milner AM, Brown LE, Hannah DM (2009) Hydroecological response of river systems to shrinking glaciers. Hydrological Processes 23: 62–77

Mykrä H, Heino J (2017) Decreased habitat specialization in macroinvertebrate assemblages in anthropogenically disturbed streams. Ecological Complexity 31: 181–188.

Ohmura A (2012) Enhanced temperature variability in high altitude climate change. Theoretical and Applied Climatology 110: 499–508.

Oksanen JF, Blanchet G, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Gavin LS, Solymos P, Stevens MHH, Szoecs E, Wagner H (2018) vegan: Community Ecology Package. R package version 2.4-6. https://CRAN.R-project.org/package=vegan

Pauls SU, Nowak C, Balint M, Pfenninger M (2013) The impact of global climate change on genetic diversity within populations and speices. Molecular Ecology 22: 925–946

Rabinowitz D (1981) Seven forms of rarity. Pp. 205–217 in *Biological aspects of rare plant conservation* (eds. H Synge and J Chichester). John Wiley and Sons, New York

R Core Team (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

605 Resh VH, Beche LA, McElravy EP (2005) How common are rare taxa in long-term benthic
606 macroinvertebrate surveys? Journal of the North American Benthological Society 24:
607 976–989
608 Robinson CT, Burgherr B, Malard F, Tockner K, Uehlinger U (2003) Pp. 259–272 In *Ecology of*
609 *a Glacial Flood Plain* (J.V. Ward and U. Uehlinger eds.). Kluwer Academic Publishers,
610 The Netherlands
611 Robinson CT, Kawecka B, Fureder L, Peter A (2010) Biodiversity of flora and fauna in Alpine
612 waters. Bundi U. (ed). Alpine Waters. Handbook Environmental Chemistry 6: 193–223
613 Robinson CT, Matthaei S (2007) Hydrological heterogeniety of an alpine stream/lake network in
614 Switzerland. Hydrological Processes 21: 3146–3154
615 Robinson CT, Thompson C, Freestone M (2014) Ecosystem development of streams lengthened
616 by rapid glacial recession. Fundamental and Applied Limnology 185: 235–246
617 Robinson CT, Thompson C, Lods-Crozet B, Alther R (2016) Chironomidae diversity in high
618 elevation streams in the Swiss Alps. Fundamental and Applied Limnology, 188: 201–213
619 Robinson CT, Tonolla D, Imhof B, Vukelic R, Uehlinger U (2015) Flow intermittency, physico-
620 chemistry and function of headwater streams in an Alpine glacial catchment. Aquatic
621 Sciences 78: 327–341
622 Saether OA (1995) *Metriocnemus* van der Wulp: Seven new species, revision of species, and
623 new records (Diptera : Chironomidae). Annales de Lomnologie 31: 35–64
624 Sarremejane R, Mykrä H, Huttunen KL, Mustonen KR, Marttila H, Paavola R, Sippel K,
625 Veijalainen N, Muotka T (2018) Climate-driven hydrological variability determines inter-
626 annual changes in stream invertebrate community assembly. Oikos 127: 1586–1595
627 Schmid PE (1993) A key to the larval Chironomidae and their instars from Austrian Danube
628 region streams and rivers. Part 1: Diamesinae, Prodiamesinae and Orthocladiinae. Wasser
629 und Abwasser Suppl. 3/93: 1–513
630 Serra-Tosio B (1989) Révision des espèces oust-paléarctiques et néarctiques de *Boreoheptagyia*
631 Brundin avec des clés pour les larves, les nymphes et les imagos. Spixiana 11: 133–173
632 Sgarbi LF, Melo AS (2018). You don’t belong here: explaining the excess of rare species in
633 terms of habitat, space and time. Oikos 127: 497–506

634 Shama LNS, Kubow KB, Jokela J, Robinson CT (2011) Bottlenecks drive temporal and spatial
635 genetic responses in alpine caddisfly metapopulations. BMC Evolutionary Biology 11:
636 278–293
637 Smith MD, Knapp AK (2003) Dominant species maintain ecosystem function with non-random
638 species loss. Ecology Letters 6: 509–517
639 Sorg A, Bolch T, Stoffel M, Solomina O, Beniston M (2012) Climate change impacts on glaciers
640 and runoff in Tien Shan (Central Asia). Nature Climate Change 2: 725–731
641 Southwood TRE (1977) Habitat, the templet for ecological strategies. Journal of Animal Ecology
642 46: 336–365
643 Southwood TRE (1988) Tactics, strategies and templets. Oikos 52: 3–18.
644 Stucki P (2010) Methoden zur Untersuchung und Beurteilung der Fliessgewässer.
645 Makrozoobenthos Stufe F. Pp. 61. Bundesamt für Umwelt (BAFU), Bern
646 Studemann D, Landolt P, Sartori M, Hefti D, Tomka I (1992) Insecta Helvetica Fauna:
647 Ephemeroptera. (W. Sauter, Ed.)
648 Tachet H, Richoux P, Bournaud M, Usseglio-Polatera P (2010) Invertébrés d'eau douce.
649 Systématique, biologie, écologie. Paris: CNRS Éditions
650 Thompson R, Townsend C (2006) A truce with neutral theory: local deterministic factors,
651 species traits and dispersal limitation together determine patterns of diversity in stream
652 invertebrates. Journal of Animal Ecology 75: 476–484
653 Tockner K, Malard F, Burgherr P, Robinson CT, Uehlinger U, Zah R, Ward JV (1997)
654 Characteristics of channel types in a glacial floodplain system (Val Roseg, Switzerland).
655 Archiv für Hydrobiologie 140: 433–463
656 Tonkin JD, Arimoro FO, Haase P (2016a) Exploring stream communities in a tropical
657 biodiversity hotspot: biodiversity, regional occupancy, niche characteristics and
658 environmental correlates. Biodiversity Conservation 25: 975–993
659 Tonkin JD, Stoll S, Jähnig SC, Haase P (2016b) Contrasting metacommunity structure and beta
660 diversity in an aquatic-floodplain system. Oikos 125: 686–697
661 Tonkin JD, Heino J, Altermatt F (2018) Metacommunities in river networks: The importance of
662 network structure and connectivity on patterns and processes. Freshwater Biology 63: 1–
663 5

664 Uehlinger U (1991) Spatial and temporal variability of the periphyton biomass in a prealpine
665 river (Necker, Switzerland). Archiv für Hydrobiologie 123: 219–237
666 Ward JV (1994) Ecology of alpine streams. Freshwater Biology 32: 277–294
667 Waringer J, Graf W (2011) Atlas of Central European Trichoptera Larvae. Vienna, Austria.
668 Whittaker RH (1956) Vegetation of the Great Smoky Mountains. Ecological Monographs 26: 1–
669 80
670 Whittaker RH (1972) Evolution and measurement of species diversity. Taxon 21: 213–251
671 Wiederholm T (1983) Chironomidae of the Holarctic region. Keys and Diagnoses. Part 1.
672 Larvae. Entomologica Scandinavica Suppl. 19: 1–449
673 Wiederholm T (1986) Chironomidae of the Holarctic region. Keys and Diagnoses. Part 2. Pupae.
674 Entomologica Scandinavica Suppl. 28: 1–482.1983
675 Wilson MJ, McTammany ME (2016) Spatial scale and dispersal influence metacommunity
676 dynamics of benthic invertebrates in a large river. Freshwater Science 35: 738–747
677 Zar JH (1984) Biostatistical Analysis, 2nd edition. Prentice-Hall Inc., Englewood Cliffs, NJ
678

679 TABLE 1. Environmental characteristics of the study streams in each catchment. Data summarized as means, standard deviations (SD),
680 and coefficients of variation (CV). Number in parentheses is the number of tributaries sampled in each catchment (see Figure 1).
681 DOM = dissolved organic matter, BOM = benthic organic matter. Asterisks (*) indicate streams significantly differed among
682 catchments (ANOVA, $p < 0.05$). Note: Abbreviations of measured variables in parentheses

Catchment		Elevation* (elev) (m a.s.l.)	Conductivity (cond) (μScm^{-1})	Temperature* (temp) (°C)	Turbidity (NTU)	DOM (mgl^{-1})	Sulfate (sulf) (mgl^{-1})	Silicate* (sili) (mgl^{-1})	Ortho-phosphate* (opho) (μgl^{-1})	Total P (tpho) (μgl^{-1})	Discharge (disc) (m^3s^{-1})	Periphyton (AFDM gm^{-2})	BOM (bom) (AFDM g/sample)
Total	Mean	2074	44	8.0	5.4	0.52	9.5	4.9	1.4	4.8	0.20	35.0	0.42
	SD	150	24	3.5	8.3	0.41	10.1	1.8	0.9	3.5	0.32	25.3	0.39
Lang (9)	Mean	1972	63	5.4	6.8	0.82	15.1	5.9	2.4	6.9	0.08	33.3	0.63
	SD	123	35	3.2	9.7	0.76	12.4	1.4	1.3	5.5	0.10	16.4	0.58
Jöri (9)	Mean	2222	53	7.8	6.9	0.44	19.7	5.2	1.3	2.9	0.26	21.1	0.44
	SD	219	18	1.6	10.2	0.19	10.4	1.0	0.9	2.1	0.42	15.9	0.30
Morteratsch (5)	Mean	2026	21	9.3	NA	0.51	2.5	4.0	0.9	2.7	0.33	35.3	0.54
	SD	42	8	1.7	NA	0.27	0	0.5	0.6	2.6	0.27	12.4	0.49
Roseg (10)	Mean	2090	44	7.6	NA	0.46	4.3	5.3	1.4	6.2	0.10	45.5	0.34
	SD	76	19	3.1	NA	0.26	2.6	2.8	0.3	2.4	0.08	37.2	0.38
Stein (8)	Mean	2064	35	11.8	2.2	0.35	2.8	3.7	0.9	5.7	0.08	38.9	0.22
	SD	107	14	3.9	2.1	0.19	0.9	1.5	0.5	1.6	0.12	28.5	0.16

683

684 TABLE 2. Summary of the number of individuals, taxa richness, Shannon's Index (H'),
685 Simpson's Index (1-D), Whittaker's $ß_w$ (beta diversity) and Lande's $ß_a$ (absolute species
686 turnover) for each catchment (number of streams sampled in each catchment in
687 parentheses).

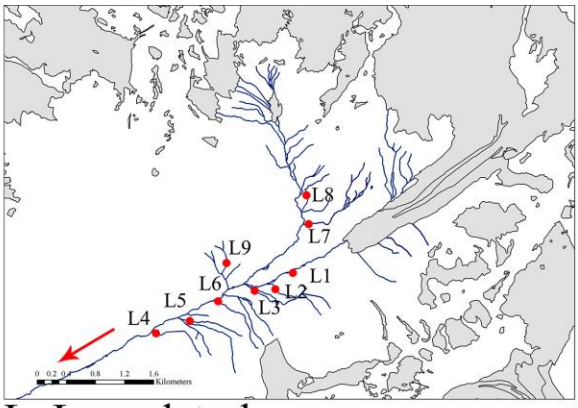
688

Catchment		Individuals	Taxa richness	Shannon's H'	Simpson's 1-D	Whittaker's $ß_w$	Lande's $ß_a$
Lang (9)	Mean	879.8	22.7	2.02	0.76	0.60	12.6
	SD	768.3	11.1	0.69	0.21	0.19	3.1
	Range	18-2539	7-33	0.63-2.75	0.24-0.91	0.30-0.88	4-17
Jöri (9)	Mean	774.6	26.3	2.35	0.85	0.43	11.3
	SD	512.4	3.0	0.22	0.06	0.09	2.5
	Range	288-1666	21-30	2.05-2.58	0.73-0.89	0.22-0.64	6-18
Morteratsch (5)	Mean	860.4	18.2	1.98	0.78	0.58	10.6
	SD	987.8	8.1	0.28	0.08	0.11	3.8
	Range	70-2501	11-32	1.56-2.25	0.66-0.87	0.42-0.72	6-16
Roseg (10)	Mean	797.9	19.5	1.88	0.72	0.54	10.4
	SD	694.3	5.1	0.68	0.24	0.12	2.3
	Range	198-2376	7-24	0.32-2.61	0.11-0.91	0.28-0.78	6-18
Stein (8)	Mean	747.6	21.0	1.93	0.77	0.49	10.4
	SD	614.2	4.6	0.26	0.07	0.10	2.7
	Range	322-2234	14-29	1.48-2.25	0.65-0.86	0.28-0.69	5-16

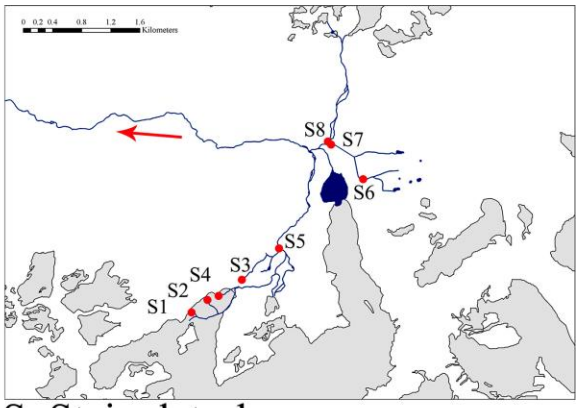
689 **Figure Legends**

690 Figure 1. Maps of the glacial catchments (L, M, R, S, J) and the corresponding stream network
691 and lakes (dark blue). Glaciers (grey) and flow directions (red arrows) together with all sampling
692 sites (red dots) are shown. All catchment maps show the same scaling and are northwards
693 oriented. Note: Glacial snout positions are drawn for the year 2008 since no newer data were
694 available, thus sites S1, S2 and S4 are ice covered in the figure but were accessible in 2012.
695
696 Figure 2. Nonmetric multidimensional scaling (NMDS) of the community data reveals subtle
697 differences between catchments in taxa composition. The adjacent Morteratsch and Roseg
698 catchments show very similar communities, whereas the other catchments differ from each other.
699
700 Figure 3. The distance-based redundancy analysis (dbRDA) shows a significant impact of the
701 environmental variables on the community dissimilarity, clustering them mainly along the
702 temperature and elevation gradient. Spatially close communities cluster only partially in the
703 dbRDA, supporting the importance of environment on community composition.
704
705 Figure 4. Comparing the observed rank-abundance data (black dots) with simulated log-normal
706 (red line) or log-series (blue line) distributions showed that the data were almost perfectly log-
707 normal distributed, indicating less rare species than expected. However, there was still an excess
708 of single findings and a slight excess of very common species.
709
710 Figure 5. Distance to the glacier (as a surrogate for stream age) explains the fraction of rare
711 species occurring at single sites. The red line shows a quasi-binomial GLM, with 95%

712 confidence intervals shown as shading. A Beta regression (blue dotted line) showed almost
713 exactly the same highly significant pattern ($R^2 = 0.374$). Different sites are colored according to
714 the catchment of origin.



L: Langgletscher



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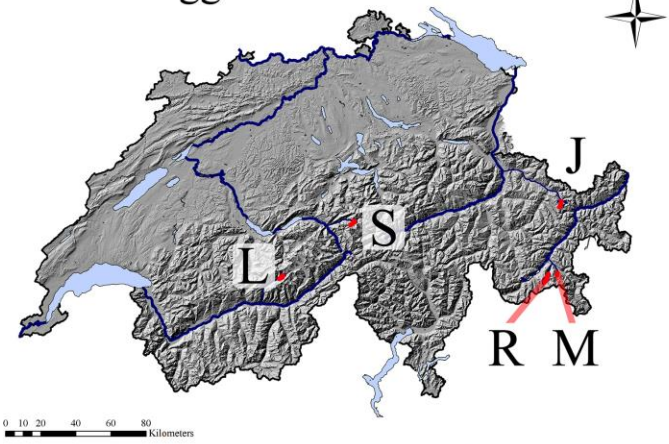
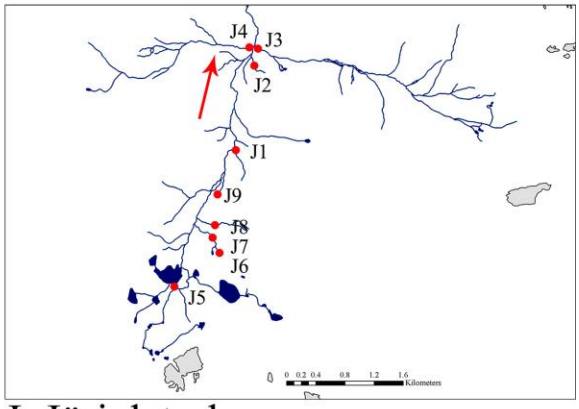
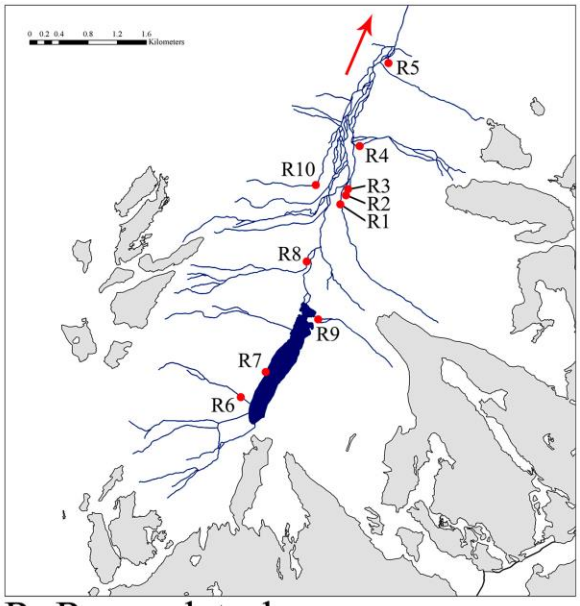
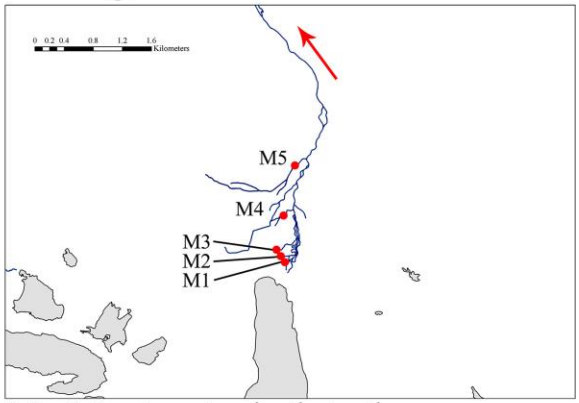




J: Jörigletscher

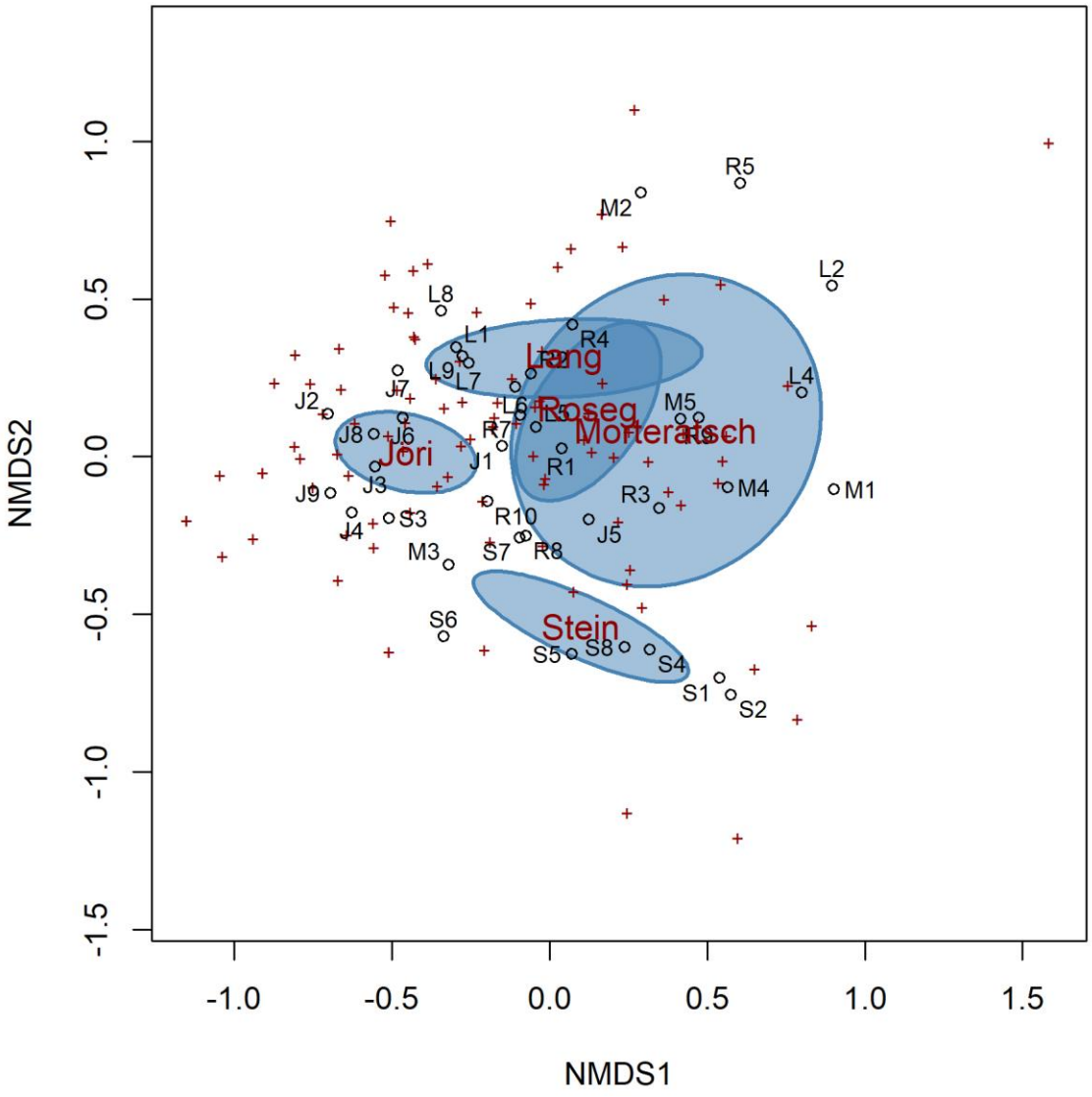


R: Roseggletscher



M: Morteratschgletscher

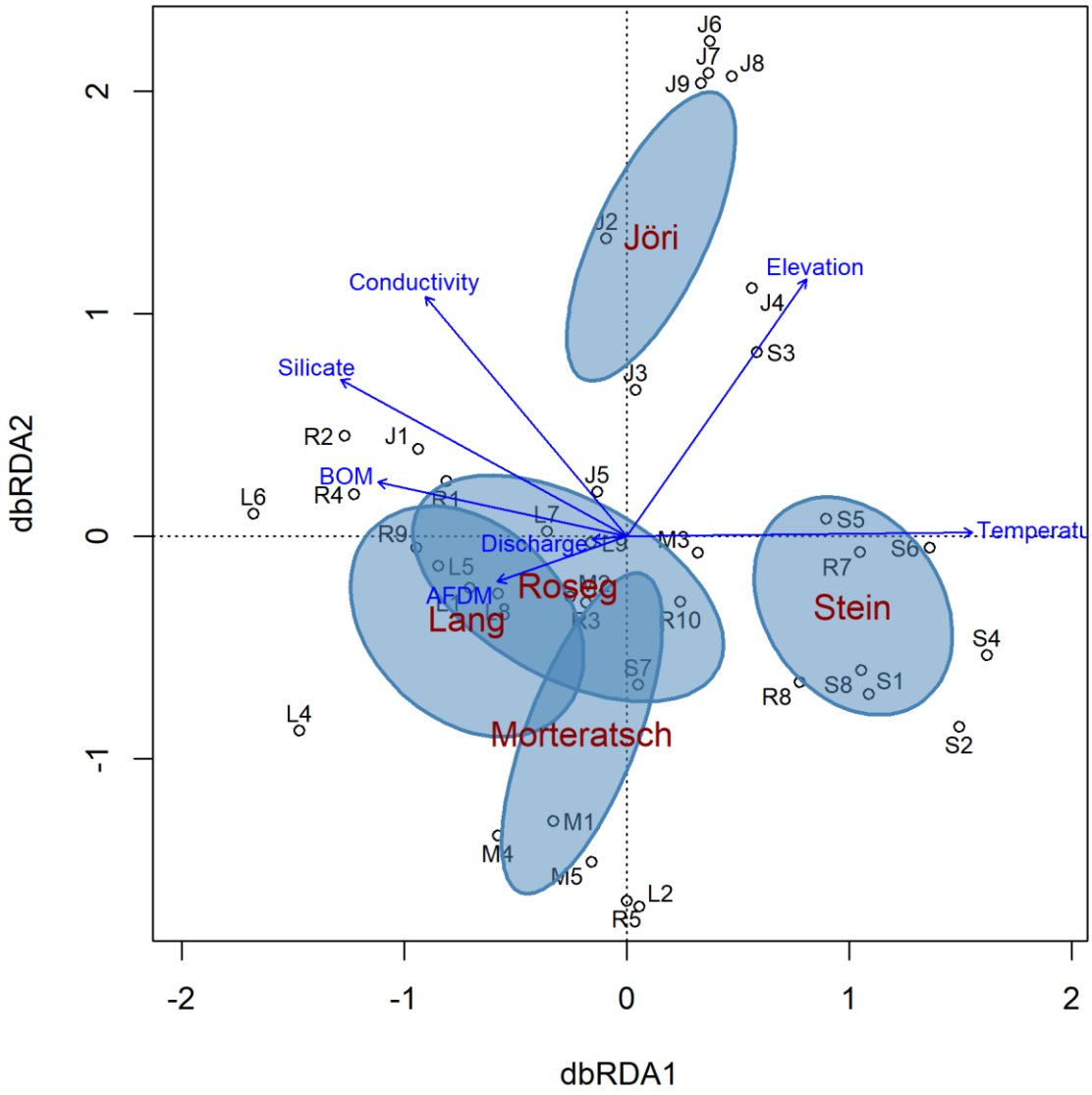
715 Figure 1



716

717 Figure 2

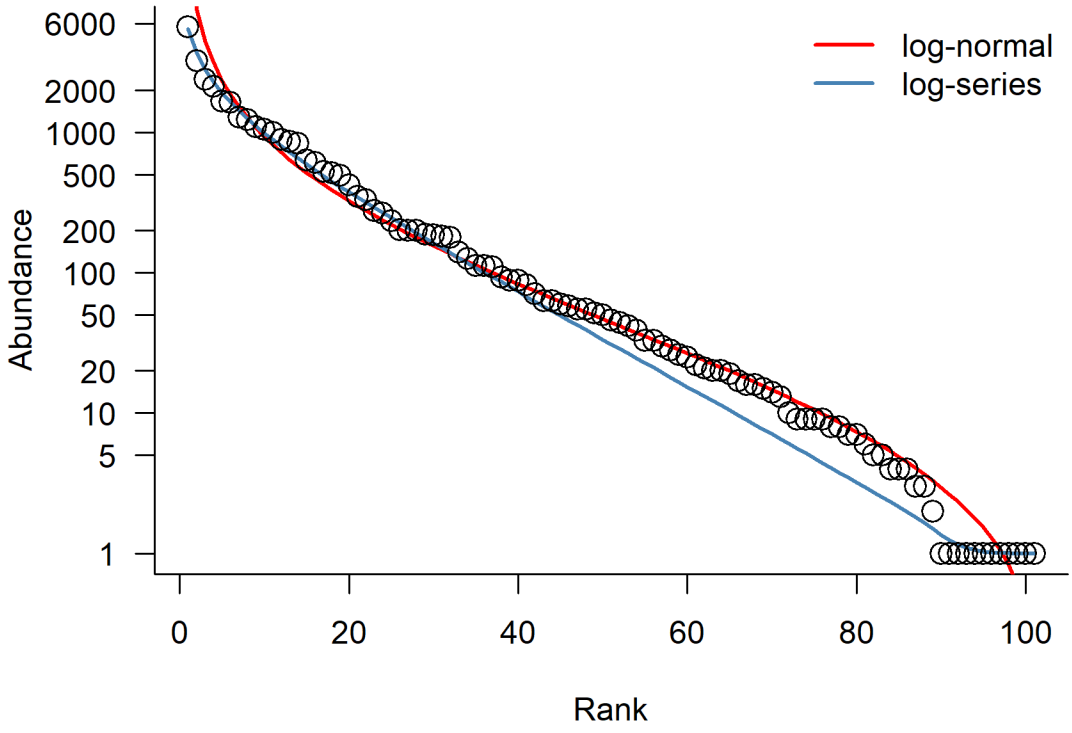
718



719

720 Figure 3

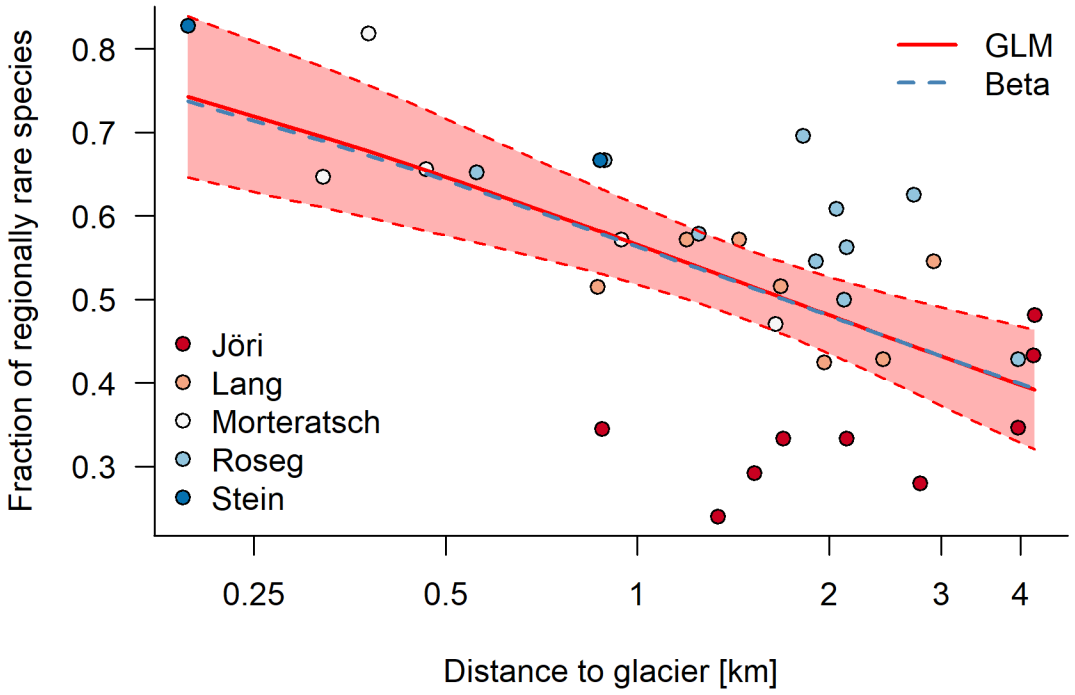
721



722

723 Figure 4

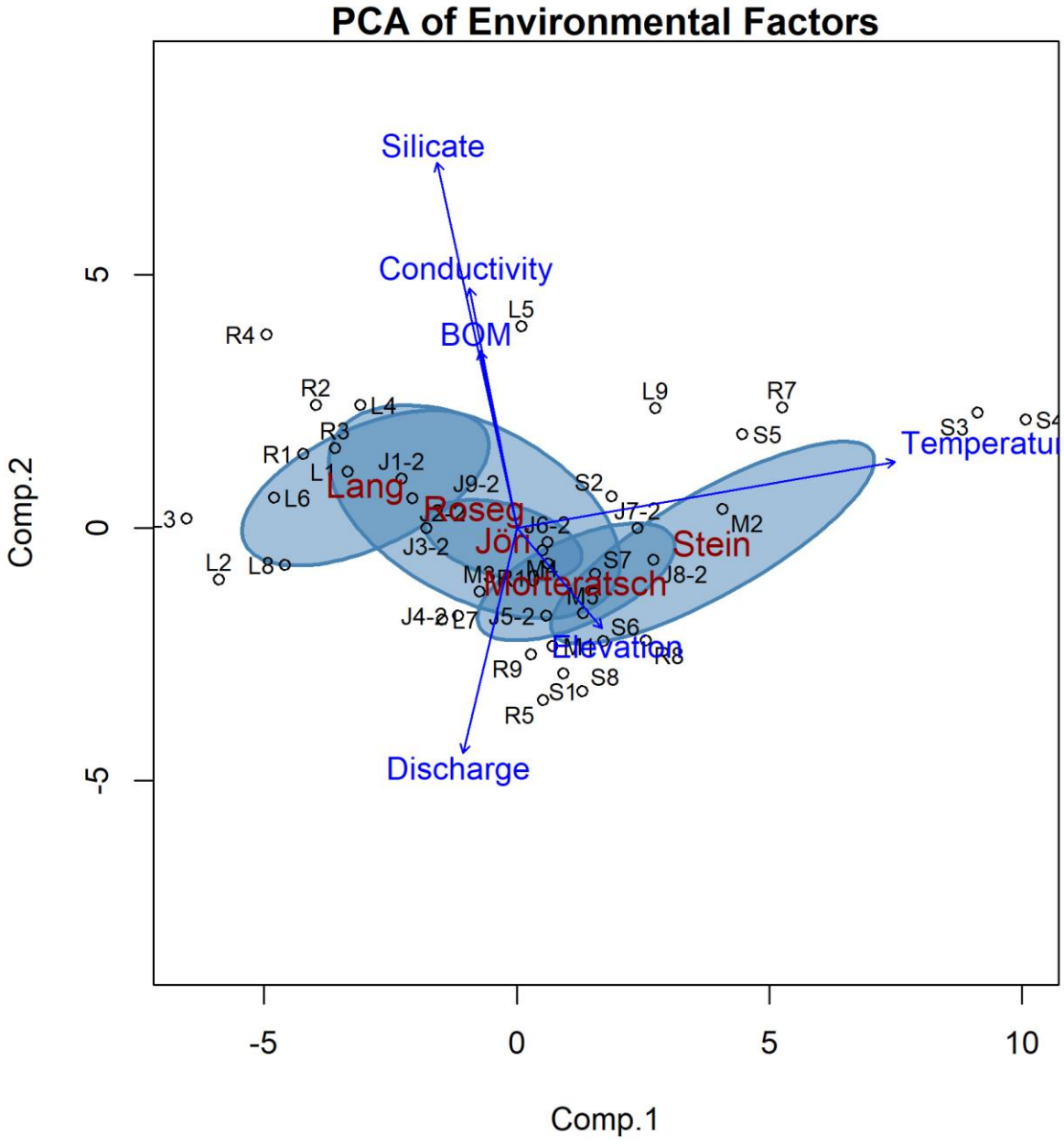
724



725

726 Figure 5

727 Figure S1. Summary plot of the principal components analysis (PCA) completed using environmental
728 measures collected for the study. Measures used in the PCA included elevation, electrical conductivity,
729 temperature, silicate, discharge and benthic organic matter (BOM).

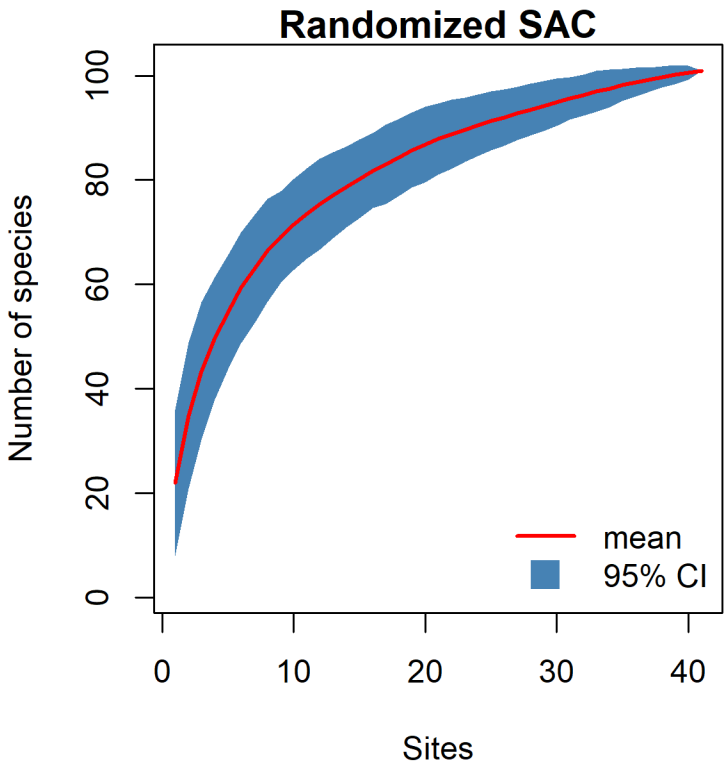


730

731

732 Figure S2. Taxon accumulation curve created by adding sites randomly and doing 100 permutations.

733 Richness saturation was not reached using 41 sites, but only few more species would be expected.



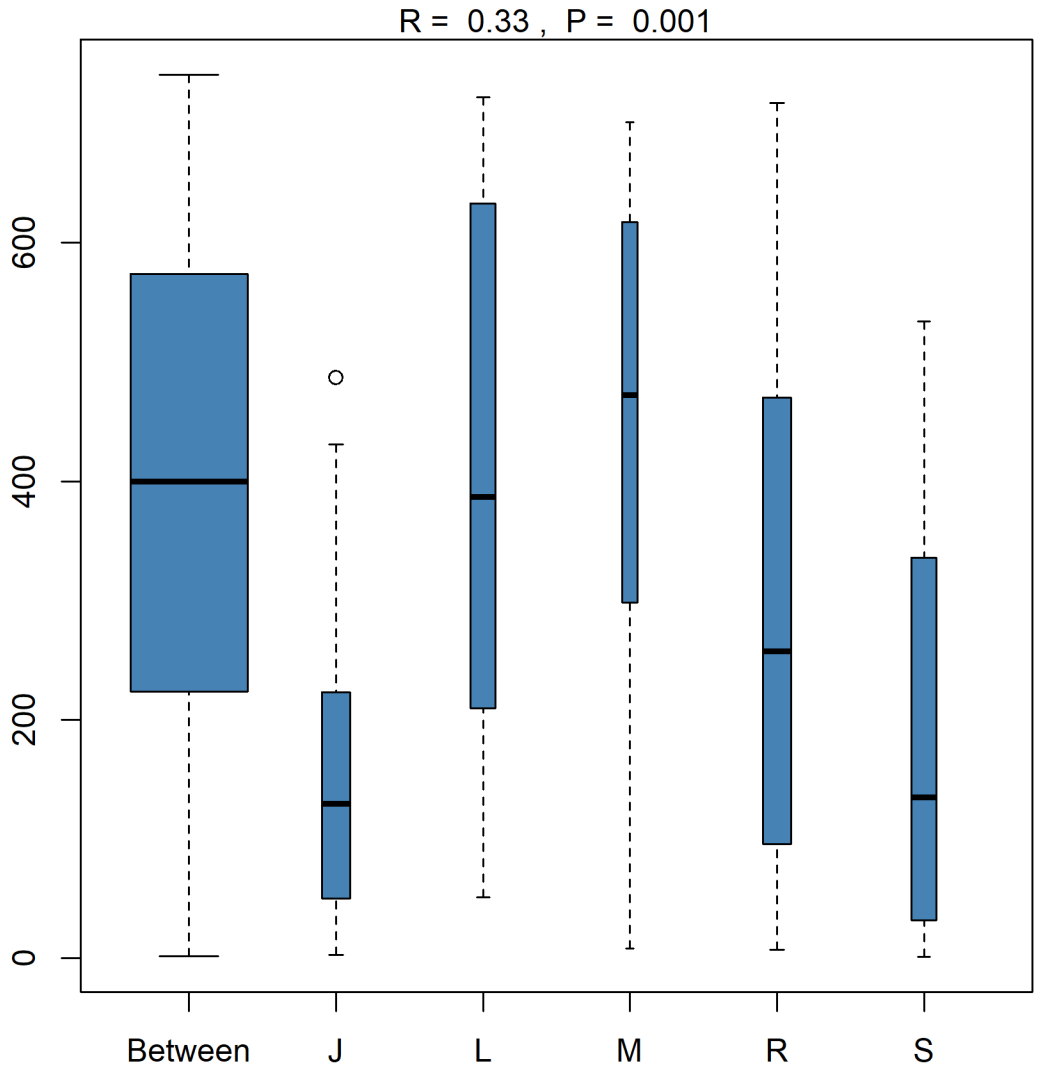
734

735

736 Figure S3. ANOSIM showing subtle but significant differences among catchments based on the Bray-

737 Curtis community dissimilarity. However, differences within and between sites fall into the same range.

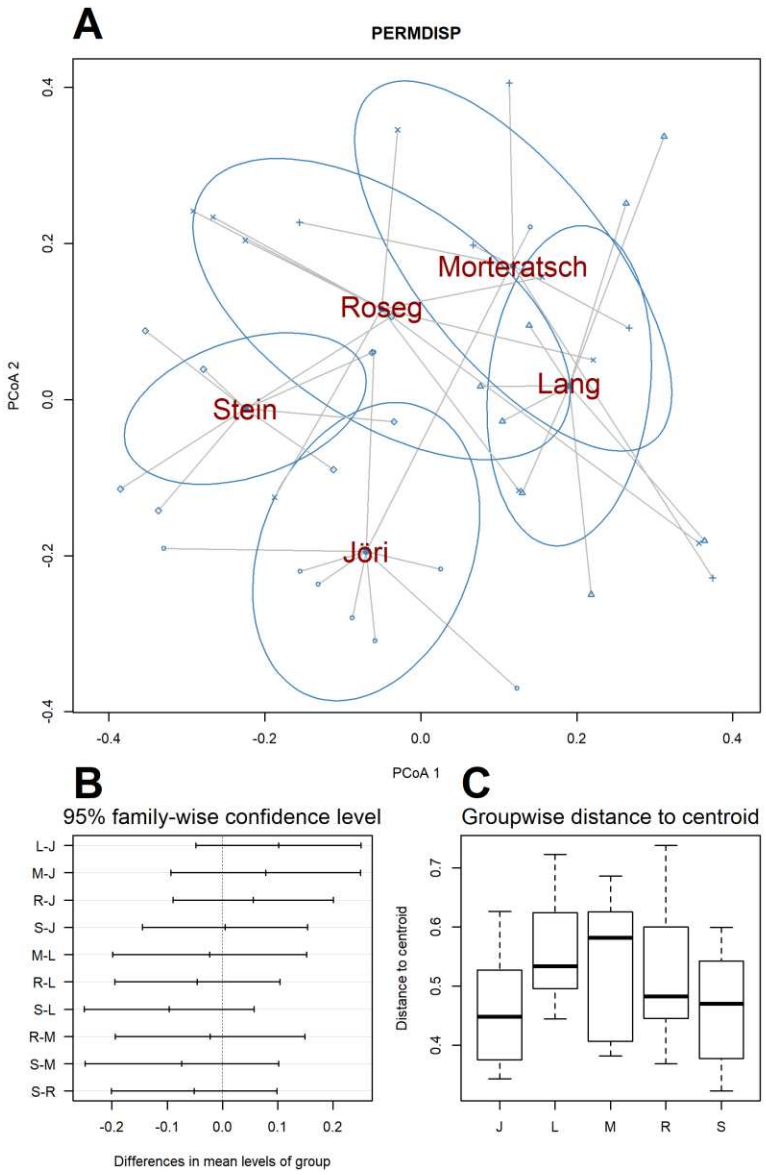
738 Width of the bars show the differences in number of comparisons.



739

740

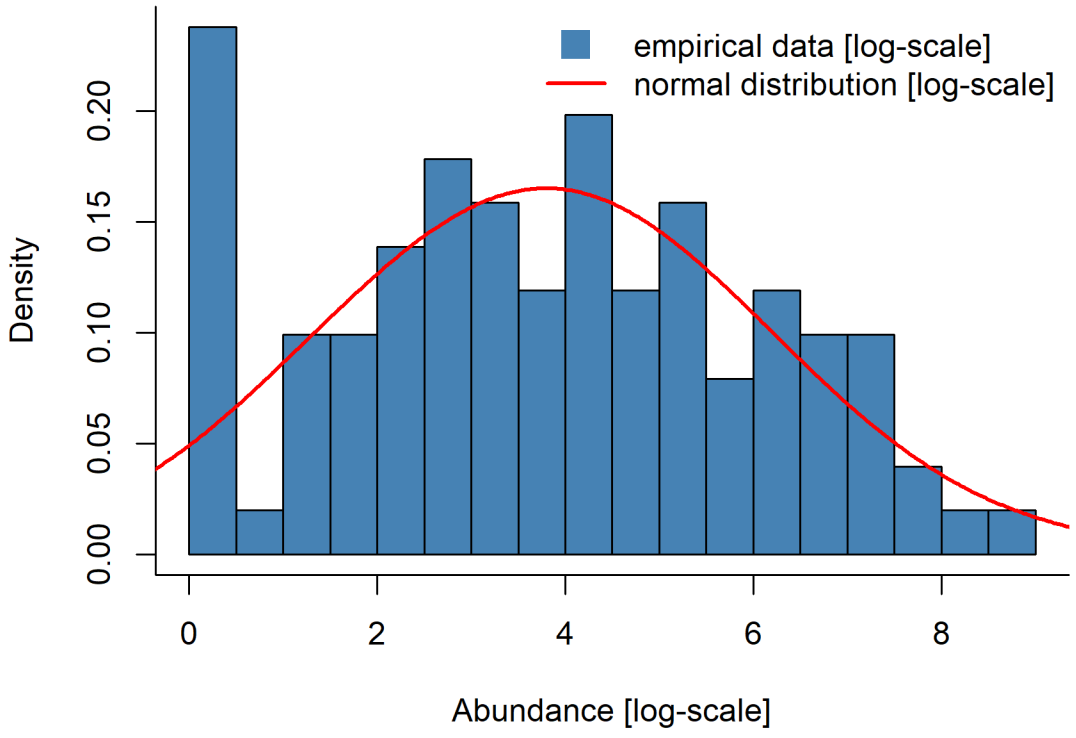
741 Figure S4. PERMDISP revealed no significant difference in β-diversity among catchments, suggesting
742 differences within catchments are comparable to among catchment differences in community
743 composition. A) Plotting PCoA 1 and 2 shows overlaps of the 95% confidence hulls around the centroids
744 of individual catchments. B) This is supported by Tukey's Honest Significant Differences (Tukey's HSD)
745 between all pairs of combinations. C) The mean distance of sites to the catchment centroid was
746 comparable among all catchments.



747

748

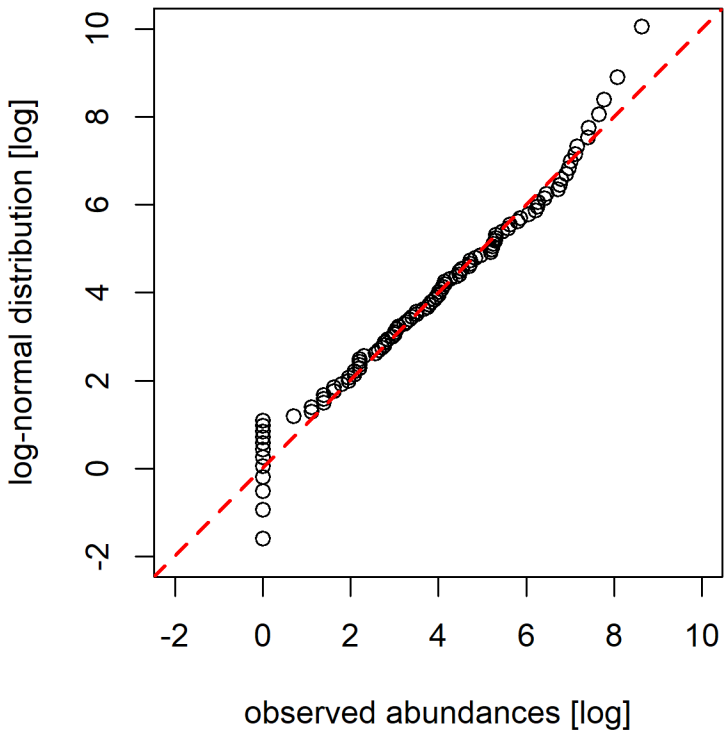
749 Figure S5. Histogram of observed abundances, with the log-normal distribution overlaid, depicting the
750 excess of single findings to the very left and a slight excess of common species at the right tail of the
751 distribution.



752

753 Figure S6. QQ-plot of observed abundances against theoretically expected values from the log-normal
754 distribution where the excess of single findings at the lower left end and a slight excess of common
755 species at the upper right end become apparent.

756



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